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## Intraspecific variation in seed yield of soybean (*Glycine max*) in response to increased atmospheric carbon dioxide

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**Abstract.** The growth characteristics of six and the reproductive development of five soybean [*Glycine max* (L.) Merr.] cultivars were examined at 39 Pa (ambient) and 70 Pa (elevated) CO<sub>2</sub> partial pressures in temperature-controlled glasshouses. Significant intraspecific variation for both growth and seed yield in response to elevated CO<sub>2</sub> was observed among the cultivars. At elevated CO<sub>2</sub>, total biomass increased an average of 42% at the end of the vegetative stage, while average seed yield increased by only 28%. No changes in % protein or % oil were observed for any cultivar at elevated CO<sub>2</sub>, relative to ambient CO<sub>2</sub>. The relative enhancement of either vegetative or reproductive growth at elevated CO<sub>2</sub> was not correlated with changes in the absolute or relative increase in single leaf photosynthetic rate among cultivars at elevated CO<sub>2</sub>. For soybean, the greatest response of seed yield to elevated CO<sub>2</sub> was associated with increased production of lateral branches, increased pod production or increased seed weight, suggesting different strategies of carbon partitioning in a high CO<sub>2</sub> environment. Data from this experiment indicates that differences in carbon partitioning among soybean cultivars may influence reproductive capacity and fecundity as atmospheric CO<sub>2</sub> increases, with subsequent consequences for future agricultural breeding strategies.

**Keywords:** climate change, CO<sub>2</sub> partial pressure, soybean, intraspecific variation, seed yield.

### Introduction

As atmospheric CO<sub>2</sub> increases (Houghton *et al.* 1996), significant increases in growth may occur for a wide range of cultivated and native plant species. However, the relative growth response to CO<sub>2</sub> will vary with species, and interspecific differences in the growth response to increasing CO<sub>2</sub> are well documented (cf. Cure and Acock 1986; Kimball *et al.* 1993).

In agriculture, intraspecific rather than interspecific variability could be used to select for optimal cultivars which would amplify reproductive output and commercial yield in an enriched CO<sub>2</sub> environment. It has been argued that empirical selection for yield will automatically choose the most CO<sub>2</sub> responsive plants over time (Kimball 1985); however, yield is dependent on many abiotic and biotic factors and, to date, little effort has focused on CO<sub>2</sub> per se as a potential selection factor in traditional breeding methods (Hall and Allen 1993). Previous work with cultivars of cowpea (*Vigna unguiculata* (L.) Walp; Ahmed *et al.* 1993), rice (*Oryza sativa* L.; Ziska *et al.* 1996) and wheat (*Triticum aestivum* L.; Manderschied and Weigel 1997) indicated that lines were available which could maximize productivity as atmospheric CO<sub>2</sub> increases. However, the morphological, phenological or physiological basis for observed increases in seed or pod yield with increased atmospheric CO<sub>2</sub> have not been fully elucidated.

Increased interest in and use of soybean products has caused worldwide soybean production to continually expand. High soybean yields reflect, in part, the multi-year efforts of soybean breeders to maintain high reproductive output over a wide range of changing environmental conditions. Given the ongoing increase in atmospheric CO<sub>2</sub>, can the additional carbon be utilized to increase seed yield in soybean by intraspecific selection within agronomically important cultivars? Previous work with soybean (cv. Bragg) in a high CO<sub>2</sub> environment indicated a reduction in harvest index (i.e. less carbon partitioned into reproductive yield) over a range of growth temperatures (Baker *et al.* 1989). This suggests that present day soybean cultivars may not be as responsive to increasing atmospheric CO<sub>2</sub> in terms of biomass production or economic yield as cultivars specifically adapted to elevated CO<sub>2</sub>. Consequently, opportunities may exist to select for maximum reproductive responsiveness among soybean cultivars in a high CO<sub>2</sub> environment. Optimizing reproductive responsiveness in turn, may depend on key physiological and morphological issues related to biomass allocation between vegetative growth and seed yield as CO<sub>2</sub> increases.

In the current study we examined the growth characteristics of six and reproductive characteristics of five soybean cultivars differing in morphology and maturity group. The primary objective of this study was to determine whether

intraspecific variation in seed yield existed among soybean cultivars in response to increasing carbon dioxide levels and, if present, to identify those physiological or morphological traits associated with maximal reproductive output.

## Materials and methods

### Experimental treatments

Soybean was grown from sowing until maturity from late March through July 1997 (Experiment 1) and again from August through early December (Experiment 2) in two glasshouses located at the USDA-ARS Climate Stress Laboratory in Beltsville, MD. Each glasshouse is 13.5 m<sup>2</sup> in floor surface area and transmits 65% of incoming PAR\*. Glasshouses were designed to maintain maximum and minimum temperatures between 31 and 17°C, respectively. Air temperature was monitored using shielded, aspirated thermocouples located near the top of plants in each glasshouse. Blowers circulated air continuously through heat exchangers which produced an air speed of ca 0.5 m s<sup>-1</sup>. Relative humidity inside the glasshouses was not controlled, but was at or near that of ambient outside air. Carbon dioxide partial pressure was controlled in both the ambient and elevated CO<sub>2</sub> glass house 24 h day<sup>-1</sup> by a WMA2 infra-red analyser (PP systems, Haverhill, MA) which injected CO<sub>2</sub> if levels dropped below 36 and 70 Pa, respectively, for each glasshouse. CO<sub>2</sub> treatments were switched between experiments. No significant differences in average air temperature were observed between glasshouses (23.2, 23.3 and 22.2, 21.9°C for Experiments 1 and 2, respectively). Average daily PAR was 23.8 and 18.6 mol m<sup>-2</sup> for Experiments 1 and 2, respectively, with no difference in light interception between greenhouses in a given experiment. A 21 × datalogger (Campbell Scientific, Logan, UT) recorded PAR, temperature and CO<sub>2</sub> partial pressure in both glasshouses at 30 s intervals. Average 24 h values of ambient and elevated CO<sub>2</sub> partial pressure were 39.1, 68.9 Pa and 38.7, 70.3 Pa for Experiments 1 and 2, respectively. Average 24 h values were higher than expected for the ambient CO<sub>2</sub> treatment due to high (40–45 Pa) night-time CO<sub>2</sub> at this site which may have resulted from low wind speed or stable atmospheric conditions (cf. Verma and Rosenberg 1976). Average daytime ambient CO<sub>2</sub> values were typically between 36–37 Pa.

### Cultivars and growth conditions

Seed from six soybean cultivars, Avery (Maturity group IV, indeterminate), Clark (Maturity group IV, indeterminate), D70-6545 (Maturity group VI, determinate), Fiskeby (Maturity group 00, indeterminate), L-62-1579 (Maturity group IV, indeterminate) and Spencer (Maturity group IV, indeterminate) were used in both experiments. All seed except for that of D-70 was obtained from the USDA Soybean Germplasm collection in Urbana, IL. L-62-1579 is an isolate of Clark differing only in leaf shape (narrow leaflets). Seed for D70-6545, an experimental cultivar with large racemes, was developed by Dr E.E. Hartwig (USDA-ARS, Stonesville, MS) and obtained from Dr William Kenworthy (University of Maryland, College Park, MD). Three to four seeds per cultivar were sown in 25 cm diameter (11.0 L) pots filled with vermiculite for each CO<sub>2</sub> treatment. For each experiment, 24–26 pots of a given soybean cultivar were assigned to each CO<sub>2</sub> treatment. Plants from a given cultivar were grouped together but groups spaced so as to minimize mutual shading with a density of 11.1 plants m<sup>-2</sup>. Plants within a given cultivar were separated by a distance of c. 30 cm. Both individual plants and groups were rotated weekly inside a glasshouse until flowering to minimize border effects. All pots were watered daily to the drip point with a complete nutrient solution containing 13.5 mM nitrogen (Robinson 1984). All pots were thinned to one plant per pot at 10 DAS for both experiments.

### Gas exchange measurements

Single leaf photosynthesis (*A*, the rate of CO<sub>2</sub> assimilation) was determined for each cultivar at three growth intervals up to anthesis/early podfill. Measurements were made using a differential infra-red CO<sub>2</sub> analyser (model 6252, Li-Cor, Lincoln, NE) in an open system attached to two whole-leaf cuvettes. Air temperature, humidity and CO<sub>2</sub> partial pressures were set to those of the glasshouse. Supplemental lighting was provided by a GE 150-W cool-beam floodlight (GE Corp., Cleveland, OH) and assimilation values reported here were obtained at a PAR of 1600 μmol m<sup>-2</sup> s<sup>-1</sup>. Assimilation was determined for the fully expanded 2<sup>nd</sup>, 4<sup>th</sup> and 7<sup>th</sup> trifoliate leaf for six plants (three per CO<sub>2</sub> treatment) for each cultivar and CO<sub>2</sub> treatment. In addition, ambient CO<sub>2</sub> grown leaves were exposed to short-term (10–15 min) increases in CO<sub>2</sub> to elevated (70 Pa) levels. Comparisons between the short-term response of assimilation rate of ambient leaves to elevated CO<sub>2</sub> with rates of leaves grown and measured at the elevated CO<sub>2</sub> treatment were used to determine the extent of photosynthetic acclimation for each cultivar.

### Vegetative and reproductive measurements

For all cultivars, the initial harvest to determine growth was at 10 DAS in both experiments. Subsequent harvests occurred at 28–33 and 49–54 DAS (Experiment 1) and 21–25 and 37–41 DAS (Experiment 2). These harvests approximately corresponded to the initial anthesis and beginning of pod formation. Anthesis occurred earlier in Experiment 2 due to shorter day-length. Although some variation was observed among cultivars, no change in days to flowering or initial pod formation was observed at the elevated, relative to the ambient, CO<sub>2</sub> treatment for a given experiment. For each harvest eight plants for a given cultivar and CO<sub>2</sub> treatment were cut at ground level and separated into leaf laminae, stems and roots. Leaf area was determined photometrically with a leaf area meter (Li 3000, Li-Cor). Dry weights were obtained separately for leaves, stems and roots. Material was dried at 55°C for a minimum of 72 h, or until dry weight was constant, and weighed.

Seed for all cultivars was obtained at maturity. Maturity was determined when 95% of the pods on an individual plant had dried and vegetative growth had ceased. At maturity, pod number, node number, pod weight, and the average weight of 50 seed were obtained for both experiments in all cultivars and treatments. Lateral branches were counted in Experiment 2. In both experiments, Avery had outgrown the space allotted to it, reaching the ceiling of the glasshouse; consequently, it was harvested prior to maturity. Seed was sent to the National Center for Agricultural Utilization Research (NCAUR) for NIR protein and oil dry weight percentage values, obtained with a NIR food and feed analyser (Infratec, Model 1255, St Louis, MO).

### Germination and emergence

To determine if seed produced at elevated CO<sub>2</sub> influenced germination and emergence characteristics, seed collected from all cultivars and CO<sub>2</sub> treatments were sown in 3.5 L vermiculite filled pots (10 seeds in each of 10 pots per cultivar and CO<sub>2</sub> partial pressure) located inside one of two controlled environment chambers (EGC, Chagrin Falls, OH). Each controlled chamber had CO<sub>2</sub> set points of 36 Pa (ambient) and 70 Pa (elevated). All plants received 14 h of 800 μmol m<sup>-2</sup> s<sup>-1</sup> PAR from a mixture of high pressure sodium and metal halide lamps (GE, Glen Ellen, VA). Day/night temperatures were maintained at 25°C and average daily RH exceeded 60%. Temperature, CO<sub>2</sub> partial pressures and RH were monitored and recorded at 1 min intervals by an EGC network datalogger in conjunction with a PC. Seed emergence and germination was determined at 4 and again at 5 DAS. Seeds were considered germinated when the testa was broken and the radical was clearly visible.

\*Abbreviations used: DAS, days after sowing; HI, grain yield/total shoot biomass; NIR, near-infrared radiation; PAR, photosynthetically active radiation, μmol m<sup>-2</sup> s<sup>-1</sup>; RGR, relative growth rate, g g<sup>-1</sup> day<sup>-1</sup>.

### Statistical analyses

The effect of CO<sub>2</sub> treatment on the response of photosynthesis was analysed by cultivar using a Students unpaired *t*-test assuming unequal variances. Changes in vegetative and reproductive characteristics between ambient and elevated CO<sub>2</sub> treatments as a function of cultivar were made using a two-way ANOVA to examine cultivar by CO<sub>2</sub> interaction, with means separated by a least square means table. Unless otherwise stated, differences were determined as significant at the  $P \leq 0.05$  level.

## Results

### CO<sub>2</sub> assimilation

For all soybean cultivars examined, growth at elevated CO<sub>2</sub> resulted in a significant stimulation of single leaf assimilation, with an average increase of 61% (Table 1). Intraspecific variability in the response of photosynthesis was also observed between cultivars with D-70 and L-62 having the smallest and largest relative increase, respectively (46 vs. 77% at elevated relative to the ambient CO<sub>2</sub> treatment) (Table 1). A slight, but non-significant decrease ( $P=0.12$ ) in CO<sub>2</sub> assimilation between the short and long-term response to elevated CO<sub>2</sub> was observed for D-70; however, no evidence of photosynthetic acclimation was observed for any of the soybean cultivars in either experiment.

### Growth/vegetative characteristics

The relative increase in plant biomass (as determined from total biomass at anthesis) was less than that observed for single leaf photosynthesis at the elevated CO<sub>2</sub> treatment, increasing 37 and 46% on average for all cultivars in Experiments 1 and 2, respectively (Table 2). All cultivars showed a significant increase in total dry weight when grown at elevated CO<sub>2</sub>. Overall, the greatest stimulation in growth occurred for stem dry weight which showed a significant stimulation at elevated CO<sub>2</sub> for all cultivars in both experiments (+46%, Table 2).

**Table 1. Single leaf photosynthetic rates (determined as CO<sub>2</sub> assimilation) for six soybean cultivars grown at either ambient (39 Pa) or elevated (70 Pa) carbon dioxide partial pressures**

Data were taken from 20 to 50 DAS from both experiments and combined for analysis. Ambient CO<sub>2</sub> grown plants were measured at both 36 and 70 Pa CO<sub>2</sub> to determine possible photosynthetic acclimation. \* indicates a significant difference ( $P < 0.05$ ) relative to the ambient grown and measured control. Students independent *t*-test,  $n=18$

Cultivar	39/36	Grown/Measured	
		39/70	70/70
		(μmol m <sup>-2</sup> s <sup>-1</sup> )	
Avery	21.9	35.6*	35.1*
Clark	21.0	35.8*	36.0*
D-70	22.6	40.7*	33.0*
Fiskeby	24.2	38.7*	36.4*
L-62	23.4	41.0*	41.5*
Spencer	27.4	46.9*	44.8*

Growth data from both experiments, plotted as total dry weight over time (DAS), demonstrated a consistent response at a given CO<sub>2</sub> treatment for an individual cultivar, indicating that the growth response to CO<sub>2</sub> was similar between experiments (Figs 1, 2). With the exception of Fiskeby, no significant increase in growth at elevated CO<sub>2</sub> was observed during the seedling stage (i.e. prior to expansion of first trifoliate; (Figs 1 and 2). A significant increase in the initial RGR (10 to ~30 DAS) was observed at the elevated CO<sub>2</sub> when compared to the ambient CO<sub>2</sub> treatment for all cultivars (0.187 vs 0.165 g g<sup>-1</sup> day<sup>-1</sup>, respectively) except Fiskeby (0.165 and 0.163 g g<sup>-1</sup> day<sup>-1</sup>). Following 30 DAS however, no significant changes in RGR were observed for any cultivar in response to the elevated CO<sub>2</sub> treatment (data not shown).

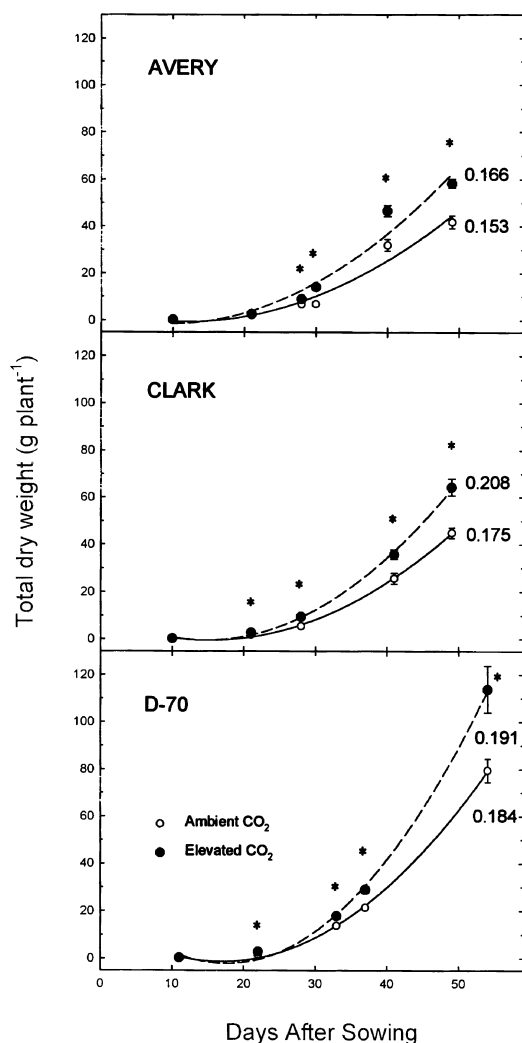
### Reproductive characteristics

Four of the five cultivars tested showed a significant increase in seed yield (g plant<sup>-1</sup>) in response to the elevated CO<sub>2</sub> treatment when averaged across both experiments (Table 3; Fig. 3). There was a significant cultivar × CO<sub>2</sub> interaction, indicating intraspecific variability of seed yield

**Table 2. Growth characteristics (on a per plant basis) for six soybean cultivars grown at either ambient (39 Pa) or elevated (70 Pa) carbon dioxide partial pressure at the end of the vegetative stage**

\* indicates a significant difference ( $P < 0.05$ ) relative to the ambient grown and measured control. Students independent *t*-test,  $n=8$

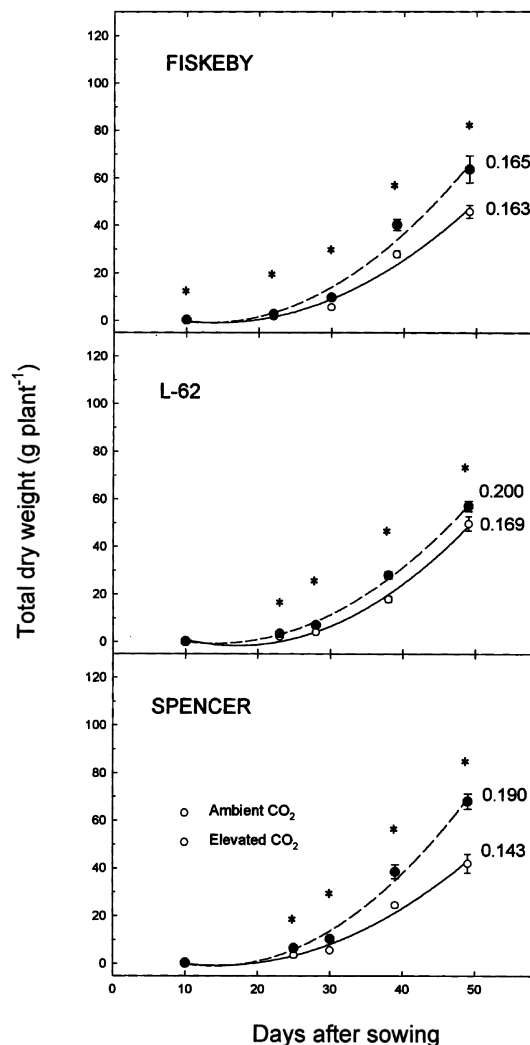
Cultivar	CO <sub>2</sub>	DAS	Leaf area	Leaf wt	Stem wt	Root wt	Total wt
	(Pa)		(cm <sup>2</sup> )			(g)	
Experiment 1							
Avery	39	49	5717	15.9	20.3	5.6	41.9
	70	49	7666*	21.6*	30.7*	6.1	58.4*
Clark	39	49	5983	18.1	18.7	7.2	45.1
	70	49	7353*	24.8*	28.9*	9.6*	64.4*
D-70	39	54	9076	31.8	36.9	10.8	79.6
	70	54	8914	51.4*	45.3*	16.5*	113.8*
Fiskeby	39	49	6741	19.3	18.7	7.1	45.8
	70	49	7308	24.8*	28.7*	9.3*	63.7*
L-62	39	49	6601	20.3	20.5	7.7	49.8
	70	49	6512	22.1	25.0*	9.2	57.1*
Spencer	39	49	5160	16.4	19.0	6.0	42.1
	70	49	8290*	23.0*	28.5*	8.3	59.8*
Experiment 2							
Avery	39	40	4562	12.3	14.2	5.5	32.0
	70	40	5781*	18.9*	19.6*	8.0*	46.6*
Clark	39	41	4567	10.9	10.6	4.1	25.6
	70	41	5918*	15.0*	15.0*	5.9*	35.9*
D-70	39	37	4853	10.2	8.3	3.0	21.4
	70	37	5321	12.4	12.4*	4.1*	29.0*
Fiskeby	39	39	5133	12.5	11.0	4.5	28.0
	70	39	6786*	16.2*	16.0*	8.1*	40.3*
L-62	39	38	3228	7.9	7.2	2.7	17.9
	70	38	4127*	12.5*	11.6*	4.0*	28.1*
Spencer	39	39	3531	10.8	9.4	4.4	24.6
	70	39	4784*	16.1*	15.4*	7.2*	38.6*



**Fig. 1.** Changes in total plant biomass for soybean cultivars, Avery, Clark and D-70 at two different  $\text{CO}_2$  partial pressures (ambient, 39 Pa and elevated 70 Pa,  $\circ$  and  $\bullet$ , respectively). Data were combined from both experiments. A second order regression was fitted to each curve. Bars are  $\pm$  SE for each point. For a given sampling date, \* indicates a significant effect of the elevated  $\text{CO}_2$  treatment ( $P < 0.05$ ) according to the Student's independent  $t$ -test,  $n=8$ . Numerical values listed by each curve represent the RGR value (determined as changes in the slope of the  $\ln$  of total dry weight from 10 to approximately 30 DAS).

in response to elevated  $\text{CO}_2$  (Fig. 3). Overall, Spencer showed the largest relative increase in seed yield in both experiments ( $\sim 48\%$ ), while D-70 indicated a positive, but non-significant response ( $\sim 13\%$ , Fig. 3). Lower absolute seed yield at either  $\text{CO}_2$  treatment was also noted for the D-70 cultivar relative to the other cultivars examined. Overall, the relative stimulation of seed yield ( $\sim 28\%$ ) among cultivars was less than that observed for biomass at flowering ( $\sim 42\%$ ) in response to elevated  $\text{CO}_2$ .

Growth at elevated  $\text{CO}_2$  was not associated with changes in the time to flowering for any cultivar in either experiment.



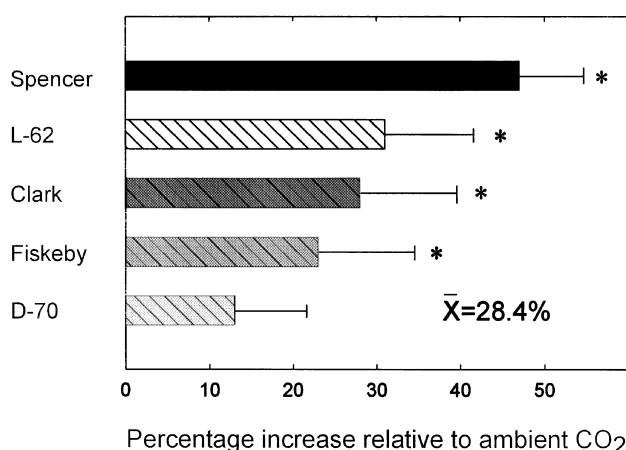
**Fig. 2.** Same as Fig. 1, but for soybean cultivars, Fiskeby, L-62 and Spencer.

There was no correlation among cultivars between the overall stimulation of biomass up through flowering and the relative change in seed yield as  $\text{CO}_2$  increased. The increased seed yield in response to elevated  $\text{CO}_2$  observed in Clark, Fiskeby and L-62 was associated primarily with increased seed weight, with a consequent increase in weight of seed per pod (i.e. a larger percentage of the total pod weight was seed), and greater pod weight (Table 3). Interestingly, for Spencer, the increase in seed yield was associated not only with an increase in seed weight, but also in pod number ( $\sim 50\%$ ), resulting from an increase in the number of lateral branches produced in an elevated  $\text{CO}_2$  environment. D-70 did show a significant increase in pods per node, but no significant change in total seed weight, presumably due to a reduction in the number of lateral branches at elevated  $\text{CO}_2$  (Table 3).

**Table 3. Reproductive characteristics (on a per plant basis) for five soybean cultivars grown at either ambient (~39 Pa) or elevated (~70 Pa) carbon dioxide partial pressure at maturity**

Seed/pod is the average seed weight per pod. Seed/pod, pod weight, 50 seed average and seed yield are given in grams per plant. Branching refers to the number of lateral branches per plant. All data from both experiments were combined for analysis except for branching, which was obtained only from the second experiment. Avery was harvested prior to maturity. \* indicates a significant difference ( $P < 0.05$ ) with respect to the ambient CO<sub>2</sub> condition for a given characteristic and cultivar. See Methods for additional details

Cultivar	CO <sub>2</sub>	Branching	Pods/ node	Pod No.	Total pod wt	50 Seed avg.	Seed/ pod	Seed yield
Clark	39	24	2.6	108	81.1	10.3	0.50	53.5
	70	26	2.9	124	103.9*	11.6*	0.56*	68.3*
D-70	39	29	2.8	113	40.8	7.5	0.20	22.2
	70	20*	4.0*	117	48.0	7.6	0.22	25.1
Fiskeby	39	27	2.4	123	89.7	9.6	0.47	58.8
	70	24	2.8	121	108.8*	13.6*	0.61*	72.4*
L-62	39	22	2.5	113	81.4	8.0	0.46	53.4
	70	22	2.9	121	104.6*	11.5*	0.59*	70.0*
Spencer	39	21	2.5	106	77.7	10.1	0.50	52.6
	70	33*	3.0	158*	122.8*	12.2*	0.52	77.4*



**Fig. 3.** The percentage stimulation of seed yield (g plant<sup>-1</sup>) for five soybean cultivars grown at elevated (70 Pa) relative to the ambient CO<sub>2</sub> treatment, least square means,  $n=16$ , bars are  $\pm$  SE.

No significant change in seed quality (specifically % protein and % oil) was observed as a function of CO<sub>2</sub> treatment, although an inverse relationship between % oil and % protein is evident among the cultivars (Table 4). The ability of seed produced at either CO<sub>2</sub> treatment to germinate and emerge was unaffected when tested at ambient and elevated CO<sub>2</sub>; however, germination and emergence rates for D-70 were significantly less than all other cultivars tested (data not shown).

### Discussion

It is clear from an increasing number of studies that intraspecific variation in growth does exist in response to increasing CO<sub>2</sub> levels (Wulff and Alexander 1985; Ziska and

**Table 4. Average % protein and % oil (g g<sup>-1</sup> dry weight) for soybean seed of five cultivars grown at ambient (39 Pa) or elevated (70 Pa) carbon dioxide partial pressures**  
Values are the mean of 10 seed from each of eight plants (80 seed total) from each cultivar from the second experiment

Cultivar	CO <sub>2</sub>	% Protein	% Oil
Clark	39	40.6	20.0
	70	41.3	19.7
D-70	39	50.5	14.2
	70	48.8	15.8
Fiskeby	39	41.6	19.8
	70	42.3	19.3
L-62	39	40.9	20.2
	70	41.0	20.6
Spencer	39	40.7	20.6
	70	40.9	20.2

Teramura 1992; Curtis *et al.* 1994; Ziska and Bunce 1995). Only a few studies, however, have quantified the range of intraspecific variability in seed or pod yield of agricultural crops in response to CO<sub>2</sub> (cowpea, Ahmed *et al.* 1993; rice, Ziska *et al.* 1996; Moya *et al.* 1998; wheat, Manderscheid and Weigel 1997). Although these initial experiments demonstrated that agronomic lines were available which could increase commercial yield as atmospheric CO<sub>2</sub> increased, the physiological and/or morphological traits associated with maximum seed yield in an elevated CO<sub>2</sub> environment have not always been fully identified.

In the current study, no correlation was observed between absolute values or relative increases of single leaf photosynthesis and seed yield for a given cultivar in response to elevated CO<sub>2</sub>. Similarly, the presence or absence of photosynthetic

acclimation at the single leaf level in response to elevated CO<sub>2</sub> was not associated with any observed stimulation of seed yield. In addition, changes in RGR, leaf area, specific leaf weight, root to shoot ratio or total biomass at flowering at elevated compared to the ambient CO<sub>2</sub> treatment were not correlated with changes in reproductive yield in response to increased CO<sub>2</sub> for any cultivar.

Although vegetative biomass was not obtained at seed maturity, due in part to leaf senescence and drop, stimulation of seed yield was only about half that of vegetative biomass (through flowering) when averaged among cultivars at the elevated relative to the ambient CO<sub>2</sub> treatment (28 vs. 42%). Previous work with soybean under controlled environment field conditions has demonstrated a reduction in HI, at 66 Pa CO<sub>2</sub>, relative to the ambient (33 Pa) CO<sub>2</sub> condition over a range of growth temperatures (Baker *et al.* 1989). Progress in increasing commercial productivity during recent decades has been made principally by increasing HI, with less emphasis on increasing shoot biomass (see Gifford 1986). Soybean cultivars which demonstrate a decrease in HI at elevated CO<sub>2</sub> may not be as well adapted as they could be to elevated CO<sub>2</sub> environments (Hall and Allen 1993).

For the soybean cultivars examined in the current study, total pod number appeared relatively fixed, with increased seed yield at elevated CO<sub>2</sub> occurring because of increased seed size. This may have accounted, in part, for the relatively small increase in seed production as CO<sub>2</sub> increased. However, for Spencer, the increase in seed yield occurred both as a result of increased seed size, but also because of an increase in lateral branching with a subsequent ~50% stimulation in pod number. For Spencer the relative increase in vegetative growth and that of seed yield were almost the same (49% and 47%, respectively), suggesting little change in HI as CO<sub>2</sub> increased.

Even for the small number of cultivars examined in the current study, partitioning of carbon within reproductive sinks had clear consequences with respect to increasing seed yield at elevated CO<sub>2</sub>. Increasing lateral branching for example, may provide additional nodes for pod production (e.g. Spencer). Similarly, increasing pods per node (assuming no decrease in lateral branching) could also be a desirable morphological trait. Plasticity in tiller production has been shown to positively influence the seed yield response to [CO<sub>2</sub>] in the field for cereal grains (Manderscheid and Weigel 1997; Moya *et al.* 1998).

Any concerted effort to determine alterations in carbon partitioning which maximize reproduction and seed yield in a future, higher CO<sub>2</sub> environment is still in its infancy. Because of the high costs of maintaining an elevated CO<sub>2</sub> environment, it is difficult to determine the full extent of intraspecific variability for large numbers of cultivars. Experiments on biomass allocation among reproductive structures in single plants in controlled environment cham-

bers or glasshouses may not mimic larger scale canopy responses in the field. In addition, other environmental interactions, especially those related to increasing air temperature, deserve further study (see Hall 1992). Yet, the additional carbon made available by the rapid increase in atmospheric CO<sub>2</sub>, and the subsequent stimulation of plant growth, can provide opportunities for breeders and physiologists to maximize future seed yield and commercial productivity. It is clear that intraspecific variation in seed yield in response to increasing atmospheric CO<sub>2</sub> exists in soybean. The extent of variation cannot be predicted from leaf photosynthesis, growth rates or vegetative parameters but may be associated with seed size, number of seeds/pod, and increased branching. Identifying the morphological, phenological and/or physiological basis for increased seed yield for individual plants in a high CO<sub>2</sub> atmosphere is a crucial first step toward field based identification of soybean cultivars that may maximize productivity in the 21st century.

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